Pliocene femur of *Theropithecus* from the Luangwa Valley, Zambia

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Key words: Zambia, Plio-Pleistocene, hominin, cercopithecoid, femur

Running title: *Theropithecus* femur from Zambia

Introduction

The Luangwa Valley in eastern Zambia has the potential to be an important source of Plio-Pleistocene fauna and archaeology, and may represent a dispersal corridor for fauna, including hominins, between eastern and southern Africa. This is highlighted by the recent discovery of a mineralised and nearly complete primate right femur, described here and attributed to *Theropithecus* cf. *darti*, that was found with stone flakes in the middle reaches of the Luangwa river valley.

Depositional context

The right femur was found in November 2001 by a local fossil collector on a sand bar of the Luangwa River, eastern Zambia (13◦12' S; 31◦42' E) (Figure 1). The bone was exposed on recent alluvial deposits of the Luangwa River after flow levels had dropped at the end of the wet season. The Luangwa River is ~ 250 m wide, meandering in planform and active, with bank erosion rates of up to 33 ma^{-1} (Gilvear *et al*., 2000). The bone was located on the surface at the upstream end of a large (>1 km long) point bar close to the main channel; this point bar is of predominantly sand size material. However, where the bone was found, low relief (maximum amplitude ~ 0.30 m) gravel fronted (maximum grain size ~ 45 mm) dune forms were present. These had migrated across the bar at an angle oblique to the main flow direction. Given the relatively coarse nature of these bedforms it is likely that they originated near the channel thalweg and then stalled under the lower flow depths experienced on the bar surface. The femur would also have been subjected to the same pattern of transport and deposition, and as a result it was not found in-situ. Because of the active nature of the Luangwa River, the bone may have been reworked on more than one occasion. However, given the completeness of the bone any reworking must have been for relatively short time periods.

Inspection of exposed banks of the Luangwa and of tributaries upstream of where the bone was found revealed no obvious location from which it may have eroded, and no other bones were found in these bank sections. It is tentatively suggested that the bone was released from sediments in the river bed as the channel eroded into them during the high flows of the wet season. The bone was fossilised under waterlogged conditions (see below) and other mineralised faunal remains have been found at the

locality. Bone bearing deposits may be located near the base of the main river channel that is approximately two metres below the dry season river level.

More than 400 stone artefacts have been collected from the site by the discoverer of the femur and these were examined in August 2002. The collection comprises flakes and cores of chert, quartz and silcrete that are primarily of Middle Stone Age typology with some Later Stone Age microlithic tools and one Oldowan core chopper. The association of the femur with stone artefacts is almost certainly fortuitous given the active flow rates of the river and the likely Pliocene age of the fossil (see below). The recent discovery of Oldowan artefacts 60 km downstream (Barham & Sambrook Smith, in prep) suggests a Plio-Pleistocene hominin presence in the Luangwa valley. The single Oldowan artefact from the femur locality may be derived from contemporary deposits, but excavation of the river channel will be needed to demonstrate such an association.

Figure 1 here

Preservation of the specimen (Figure 2)

The shaft, femoral head, neck and intertrochanteric crest of the right femur have been preserved but there is extensive damage to the surface bone. The medial and lateral condyles lack surface bone, are missing the epicondyles and are further damaged laterally and inferiorly. The specimen also lacks the greater and lesser trochanters. There is no indication that the femur has been exposed to weathering, but much of the external bone has flaked off the distal third of the shaft, leaving an uneven mottled undersurface of bone exposed. This is similar to experimental bones preserved in weakly acid swamp conditions for periods of up to 12 years (Andrews & Amour-Chelu 1998: figure 6), where the bone becomes denatured rather than etched as it would be in more strongly acid conditions. The distal articular surface has been almost totally destroyed, and there is some indication here of acid etching and blackening by manganese deposition. There is also heavy deposition of manganese on the whole of the posterior surface of the femur, contrasting with the light brown colour of the anterior surface. The distribution of taphonomic modifications suggests deposition in a permanently wet environment in weakly acid water, with the bone stable and resting on its posterior surface. It is likely that it was not lying flat, but the

superior end was raised higher than the distal end and may have been above water for some of the time.

Figure 2 here

Description of the specimen

The specimen, a primate right femur, is cercopithecid and has features, including marked distolateral splay and anterior convexity of the shaft, that are indicative of members of the genus *Theropithecus*. The gracility of the specimen, along with the relatively long femoral neck that lacks a ridge on the anterior aspect and an oval fovea capitis suggests that the specimen has affinities to *Theropithecus darti*.

The femur, from its most proximal to its most distal extent (proximal head to distal lateral condyle), measures 265mm (Table 1), and the shaft is 198mm long. The mediolateral midshaft diameter is 14.8mm and the anteroposterior midshaft diameter is 15.2mm. The shaft is thus more gracile than is seen in *T. oswaldi* (Tables 1, 2 and 3) but the Zambian specimen has similar mediolateral and anteroposterior shaft widths to those of the *T. darti* proximal femur, AL 341-5, from Hadar (Table 2). There is a strong anterior convexity to the shaft, a feature that is found in modern *Theropithecus* but is less marked in other living cercopithecines (Jolly, 1972). The femoral shaft thickens distally, and the specimen has marked distolateral splay, even when the damage to the condyles is taken into account. This 'reverse' carrying angle, an adaptation to long periods of upright sitting during foraging, is found in both modern and fossil *Theropithecus* but is almost never observed in other cercopithecoids (Krentz, 1993).

The femoral head lacks cortical bone, but the fovea capitis is present, and is oval, angled and placed posteriorly on the femoral head. Fovea capitis morphology and position vary between cercopithecid taxa; the fovea capitis of the Zambian specimen is much more similar to the oval and posteriorly-orientated fovea capita found in *T. darti* than it is to the elongated fovea capita of *T. brumpti* and some *T. oswaldi* specimens (Krentz, 1993). The intertrochanteric crest is undamaged but incomplete, as is found in modern and fossil *Theropithecus* and some *Colobus* species, and is less prominent than the ridges observed in many large papionins. The neck length

measured from the intertrochanteric crest is difficult to report with confidence, as the preservation of the specimen makes the estimation of the position of the junction of the neck and articular surface difficult, but it is in the range of 24 – 28mm. The femoral necks of modern *Papio* and *Mandrillus* species tend to be relatively short and broad in contrast to the longer neck of *Theropithecus gelada*, with the *T. oswaldi* femoral neck being more similar to those of *Papio* and *Mandrillus* (Jolly, 1972). The relatively long neck of the Zambian specimen therefore distinguishes it from that usually observed in most large-bodied papionins, including *T. oswaldi*, but not *T. darti*, in which neck lengths are much more variable (Krentz, 1993), and generally longer than those of *T. oswaldi* specimens. Also unlike the condition seen in *Theropithecus oswaldi*, but similar to the condition in *T. darti*, the neck on the Zambian specimen does not have a ridge on its anterior aspect.

Cercopithecoid hindlimb bones are difficult to taxonomically identify with confidence, due to the broad similarities in morphology across the superfamily. Identification of the Zambian specimen is made more complex by the damage to the condyles and the greater trochanter, features of the femur that are often used to distinguish between different cercopithecid taxa (Krentz, 1993). However, the pronounced distolateral splay of the femur indicates that the specimen is very likely to be *Theropithecus* (Krentz, 1993). The inclusion of the Zambian specimen in *Theropithecus* is further supported by the anterior convexity of the shaft (Jolly, 1972), as well as the overall length of the femur, as long as is seen in many theropith specimens from East Africa, and longer than many Plio-Pleistocene and modern cercopithecid femora (Table 1). However, it should be noted that several genera of Plio-Pleistocene cercopithecids, including the colobine *Paracolobus*, were larger than many modern monkey taxa (Ting & Ward, 2001), so large size alone does not indicate that a specimen is best included in *Theropithecus*. The gracility of the specimen, its relatively long neck with a ridge on the anterior aspect, and the oval fovea capitis further indicate that the femur is *Theropithecus* cf. *darti*.

Tables 1, 2 & 3 here

Discussion

The genus *Theropithecus* was widely distributed in Africa over the course of the Plio-Pleistocene (Delson *et al*., 1993). However, to date, *Theropithecus* has not been identified from Zambia, and the specimen described here thus extends the known range of the genus in Africa. The femur is likely to be of Pliocene age, as *T. darti* is a time-sensitive species, dated to between 2.9 – 3.4 Ma at Hadar in East Africa (Eck, 1993), and to c. 3 Ma (McKee, 1995) or 2.5 Ma (Herries & Latham, 2002) at Makapansgat in southern Africa. The Zambian region is a potential dispersal corridor for East and southern African faunas, including hominins, and the specimen described here may provide evidence of early links between the East and southern African *Theropithecus* populations.

Few taxonomic assignments of cercopithecid specimens are based on postcranial material alone, and the femora of some Plio-Pleistocene cercopithecine and colobine species are very similar, due to convergence in locomotor strategies and habitat preferences (Szalay & Delson, 1979; Ting & Ward, 2001). Thus, the definite identification of *Theropithecus* from Zambia can only be made when craniodental material is recovered. However, Plio-Pleistocene *Theropithecus* femora do differ from those of other cercopithecids in a number of ways, especially in the presence of distolateral splay, a feature that is clearly evident on the Zambian specimen. Another characteristic of the Zambian femur, its gracility, may also shed some light on the evolution of locomotor behaviour in *Theropithecus*. Long bone robusticity correlates with locomotor strategy in papionins, with many terrestrial species having a more robust postcranium than those that are less terrestrial, so the gracility of the Zambian specimen suggests that it belonged to a papionin that was at least partially arboreal. Krentz (1993) argued on the basis of postcranial elements recovered from Hadar that *T. darti* was a terrestrial quadruped with some arboreal tendencies, and this appears to be supported by the evidence from the Zambian specimen. This, in combination with research demonstrating that *T. brumpti* was likely to have used arboreal substrates extensively (Krentz, 1993; Ciochon, 1993) and that *T. oswaldi* was less terrestrial than the modern species, *T. gelada* (Elton, 2002), therefore indicates that the highly terrestrial behaviour of *T. gelada* may not be representative of the genus as a whole.

In conclusion, the discovery of the femur, along with the presence of Oldowan sites further downstream, highlights the importance of the Luangwa Valley region for the study of Plio-Pleistocene hominin and cercopithecid evolution. Further investigations are planned to locate the waterlogged deposits from which the bone was derived and to assess any possible direct association with tool-making hominins.

Acknowledgements

Steve and Anna Tolan of the Chipembele Wildlife Education Centre kindly brought their discovery of the femur to our attention for which we are grateful. They also gave free access to their collections of fauna and artefacts from the locality. The Zambian National Heritage Conservation Commission expedited the granting of an export permit for the study of the femur and the British High Commission safely delivered the bone to London. Our thanks to both institutions, and to the Natural History Museum London for housing the bone during analysis. SE is grateful to Robert Kruszynski and Paula Jenkins of the Natural History Museum London, Malcolm Harman of the Powell-Cotton Museum and Dr Georges Lenglet of the Musee d' Histoire Naturelle Bruxelles for providing access to collections and assistance during the analysis of the femur. The photographic unit of the Natural History Museum provided Figure 2 and Sue Grice drafted Figure 1. We also thank an anonymous referee for their comments on this paper. Funding from the Department of Archaeology, University of Bristol, and the Arts Faculty Research Fund of the University of Bristol to LB enabled the fieldwork to take place, and analysis of the femur was supported by a Nuffield Foundation grant (NAL/00404/G) to SE.

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Table 1: Medial and lateral femoral lengths of fossil and extant cercopithecoids

	Papio anubis **n = 27**	***Colobus guereza*** **N = 30**	***Theropithecus gelada*** **n = 17**	***Paracolobus chemeroni*** **KNM-BC 3**	***Colobus* sp. KNM-ER 5896**	***Theropithecus oswaldi*** **n = 2 (medial) n = 3 (lateral)**	**Zambian specimen**
Medial length (mm)	236 ± 25	195 ± 12	187 ± 9	281	171	250 ± 20	
Lateral length (mm)	245 ± 27	197 ± 12	192 ± 10	284	174	261 ± 21	
Proximal head to distal lateral condyle (mm) *							265

*approximately equivalent to medial length

Table 2: Anteroposterior and mediolateral femoral midshaft widths of fossil and extant cercopithecoids

	Papio anubis **n= 27**	***Colobus guereza*** **n = 30**	***Theropithecus gelada*** **n = 17**	***Paracolobus chemeroni*** **KNM-BC 3**	***Colobus*** **sp. KNM-ER 5896**	***Theropithecus oswaldi*** **n = 5**	***T. darti*** **AL 341-5 (Cast)**	**Zambian specimen**
Anteroposterior width at midshaft (mm)	15.7 ± 2.2	12 ± 1.2	12.7 ± 0.8	21.2	10.6	19.1 ± 0.6	15.3*	15.2
Mediolateral width at midshaft (mm)	15.9 ± 2.1	12 ± 0.8	13.4 ± 0.9	21.0	109	19.3 ± 2.2	15.0*	14.8

*Position of midshaft estimated

Table 3: Femoral robusticity of fossil and extant cercopithecoids

	Papio anubis **n= 27**	***Colobus guereza*** **n = 30**	***Theropithecus gelada*** **n = 17**	***Paracolobus chemeroni*** **KNM-BC 3**	***Colobus* sp. KNM-ER 5896**	***Theropithecus oswaldi*** **n = 2**	**Zambian specimen**
Robusticity*	106 ± 19	75 ± 9	91 ± 9	159	67	222 ± 30	85

*Robusticity is calculated as (Mediolateral * Anteroposterior widths at midshaft) / Medial length * 100

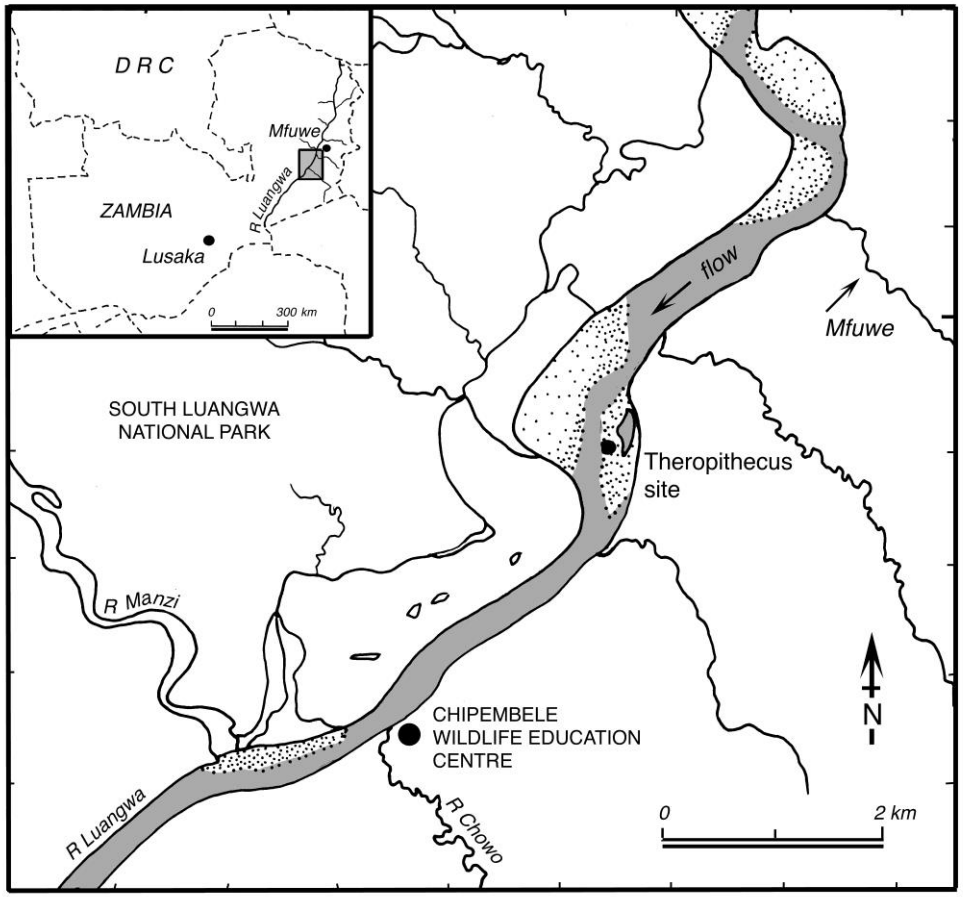

Figure 1: Geographic location of the *Theropithecus* find

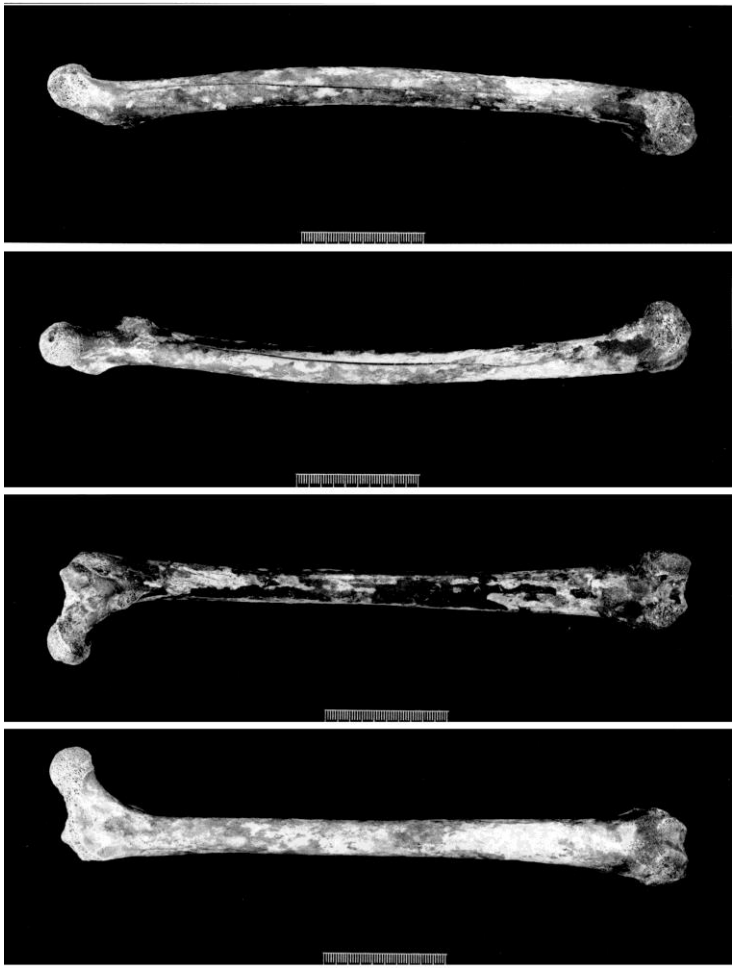

Figure 2: The *Theropithecus* cf. *darti* right femur